

A NEW DEVONIAN FERN, *FANNINGOPTERIS WYATTII*, FROM QUEENSLAND

H. TREVOR CLIFFORD

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A new fern, *Fanningopteris wyattii* gen. et sp. nov., is described from late Givetian sediments in the Cultivation Gully Formation, Burdekin Basin, northeast Queensland. □
Fanningopteris, *Stauropteridales*, fern, Devonian, Givetian.

H.T.Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 19 February 1999.

The discovery, at Cultivation Gully about 70k southwest of Townsville, of a small silicified float containing numerous, anatomically similar, permineralised fossil fern axes (Fig.1) is noteworthy for the sediments are late Givetian thereby extending by several million years the known history of pteridophytes in Australia. Previously the oldest known Australian fossil fern was portion of a false-stem of *Austroclepsis australis* (Osborn) Sahni collected from rocks of Frasnian or Famennian age in the bed of the Manilla River about 20k west of Barabba, NSW (Osborn, 1916; Sahni, 1928).

STRATIGRAPHY

The Cultivation Gully Formation in the Burdekin Basin of the Townsville hinterland consists of a series of paralic lithofelspathic sandstones, mudstones, siltstones and tuffs whose basal member was deposited in a marine environment. The specimen was collected as a float from immediately above these sediments which have been assigned a late Givetian age (380.8-377.4 Ma Harland et al., 1990) on the basis of conodonts and coral assemblages (Talent & Mawson, 1994). As the silicified float was extracted from marine sediments it must have been reworked from elsewhere and so the fern axes may be somewhat older than the age here assigned them.

Fragmentary plant remains occur throughout the Formation (Cook et al., 1994) but, other than a lycopod which has been assigned tentatively to *Schizopodium* (Henderson & Crosdale, 1998), none has been identified. Unlike the fern axes these plants are preserved as coalified impressions in siltstone.

SYSTEMATIC PALAEOONTOLOGY

Division PTERIDOPHYTA
Order STAUROPTERIDALES
***Fanningopteris* gen. nov.**

ETYMOLOGY. Greek, *pterus*, a kind of fern; Fanning River, type locality.

DIAGNOSIS. Erect, dichotomously branched rhizomatous herb with adventitious roots; all axes more or less cylindrical and anatomically similar; vascular tissue a single centrally placed cylindrical exarch protostele; in transverse section xylem strand mostly quadrangular but sometimes triangular in outline; tracheid elements indirectly attached annular or indirectly attached tilted annular; phloem alternating with protoxylem poles; pericycle narrow; endodermis a single row of rectangular cells; cortex differentiated into a narrow outer zone of thick-walled cells and a broad inner zone of thin-walled cells; sporophylls, sporangia and spores not known (Fig. 2).

***Fanningopteris wyattii* sp. nov.**
(Figs 1-6)

ETYMOLOGY. For D.H.Wyatt, for substantial contributions to the geology of North Queensland.

MATERIAL. Holotype. QMF 40510 from 70k southwest of Townsville at 19°43'S, 146° 27'E, coll. A.G. Cook.

DESCRIPTION. An erect, rhizomatous, glabrous, dichotomously branched herb; all axes anatomically similar, 1.4-4.7mm in diameter, intertwining, more or less circular in transverse section, with the perimeter interrupted by a series of low triangular projections representing vertically oriented ridges or non-vascularised enations, rarely expanded to form wings (Fig. 2); vasculature a centrally placed, circular protostele (Fig. 3), but sometimes with two steles

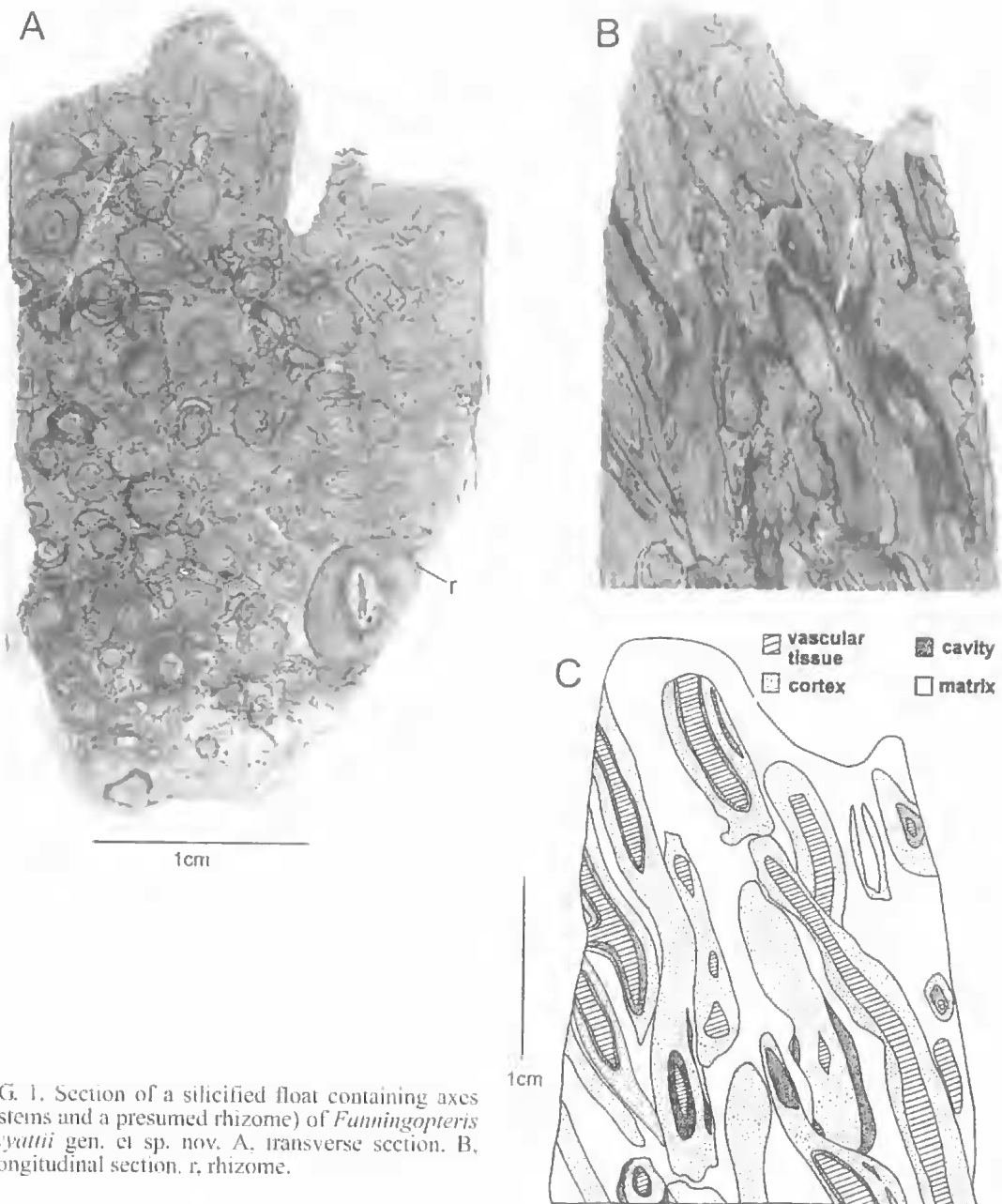


FIG. 1. Section of a silicified float containing axes (stems and a presumed rhizome) of *Fanningopteris wyattii* gen. et sp. nov. A, transverse section. B, longitudinal section. r, rhizome.

immediately below a dichotomy (Fig. 2); xylem strand quadrangular or rarely triangular (Fig. 2), with sides somewhat concave between the protoxylem poles; metaxylem tracheid elements mostly 120-140 μ m in diameter and distributed evenly throughout the tissue; protoxylem tracheid elements with diameters of 4-8 microns; phloem occupying lens-shaped areas and alternating with the protoxylem poles, presumed

sieve tubes (Fig. 3) about 40 μ m in diameter intermixed with parenchyma cells 16-20 μ m in diameter; pericycle one to a few cells wide; endodermis of rectangular parenchymatous cells (Fig. 3) with a tangential length of about 64 microns and a radial width of about 42 μ m; Casparian strip not evident (Fig. 3); cortex differentiated into two zones, a narrow outer

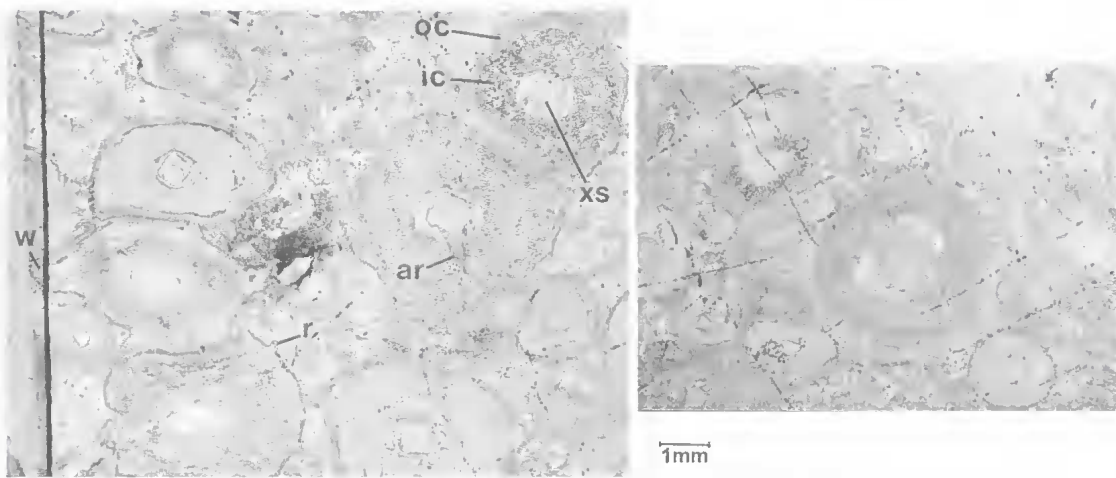


FIG. 2. Axes of *Fanningopteris wyattii* gen. et sp. nov. in transverse section. ar, adventitious root; ic, inner cortex; oc, outer cortex; r, rib; w, wing; xs, xylem strand. Note large stem with two xylem strands.

band, about four cells wide, of rectangular tangentially elongated thick-walled cells ($60 \times 20 \mu\text{m}$) and a broad inner band, 6-16 cells in width of isodiametric parenchymatous cells varying from $112\text{-}32 \mu\text{m}$ in diameter (Fig. 4A-B); airspaces lacking throughout the cortex and xylem; rhizomes up to 5.4mm in diameter and anatomically similar to axes but differing in that the cortex is not markedly differentiated into two zones (Fig. 1A); adventitious roots about 0.5mm in diameter; sporophylls, sporangia and spores not known.

In vertical section the xylem is seen to be composed entirely of annular, tilted annular or indirectly attached annular tracheid elements as

defined by Bierhorst (1960). The spacing of the annuli is independent of the diameter of the tracheid element in which they are formed and so aside from cell diameter there is no distinction between the meta- and protoxylem tissue.

The tracheid elements which resemble those of the zosterophyll *Gosslingia breconensis* (Kenrick & Edwards, 1988; Kenrick & Crane, 1997) are strengthened by the deposition on their primary walls of annuli of unknown chemical composition. The annuli vary in height from $10\text{-}12 \mu\text{m}$ and in width from $8.0\text{-}4.8 \mu\text{m}$. As seen in section the annuli expand abruptly from the primary cell wall to a maximum width and thereafter taper to an obtuse apex (Fig. 4C). In

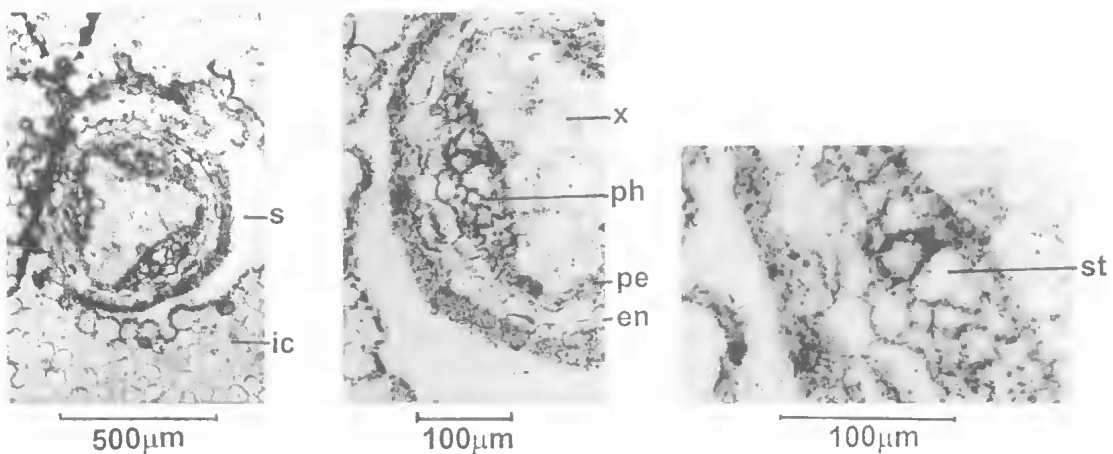


FIG. 3. Stelar anatomy of *Fanningopteris wyattii* gen. et sp. nov. in transverse section. e, endodermis; ic, inner cortex; p, pericycle; ph, phloem; st, sieve tube; xs, xylem strand.

most tracheid elements the annuli are destroyed during the process of fossilisation. However, their former presence is indicated by thin strands of magnetite which have been deposited on the primary cell walls between the bases of adjacent annuli (Fig. 5A). The strands sometimes divide (Fig. 4C,5A) which has been taken as evidence for some of the annuli being indirectly attached. None of the strands has been observed to assume the form of a spiral. The end walls of the tracheid elements are transverse or tapering (Fig. 5C) in which respect they are similar to the cells of the inner cortex (Fig. 5B). The cells of the xylem and inner cortex are mostly much longer than broad. However, due to the flexuous habit of the stems in the sections available both end walls are seen in only the shortest cells. Therefore it has not been possible to estimate the mean lengths of either the tracheid elements or the inner cortical cells.

For most fossil axes the pericycle and phloem are missing leaving the xylem strand separated from the inner cortex which is also separated from the outer cortex, especially where the axis is ribbed (Figs 1-3). The separation of the inner and outer cortex may be due to mechanical causes resulting from the different responses to compression of the two tissues one of whose cells are thick-walled cells and the other parenchymatous. The separation occurs more often immediately below the ribs rather than elsewhere around the perimeter. In contrast the separation of the inner cortex from the xylem probably results from the decay of the nutrient rich phloem and pericycle following the death of the axis. Reconstruction of a stem in cross section (Fig. 6) incorporating the anatomical features discussed above allows for the separation of the tissues in fossil specimens.

That the plant was rhizomic has not been observed directly but has been inferred from a section of an axis which is larger than the

remainder, is elliptical in outline, and whose cortex is not conspicuously differentiated into two contrasting zones (Fig. 1A). Examination of the xylem and cortex tissues reveals that the presumed rhizome has been cut obliquely. Therefore, it may be assumed the axis is circular in section and disposed more or less at right angles to the stems in the section.

As with its proposed rhizomatous habit the dichotomous branching of *Fanningopteris* has been inferred from a section in which most of the

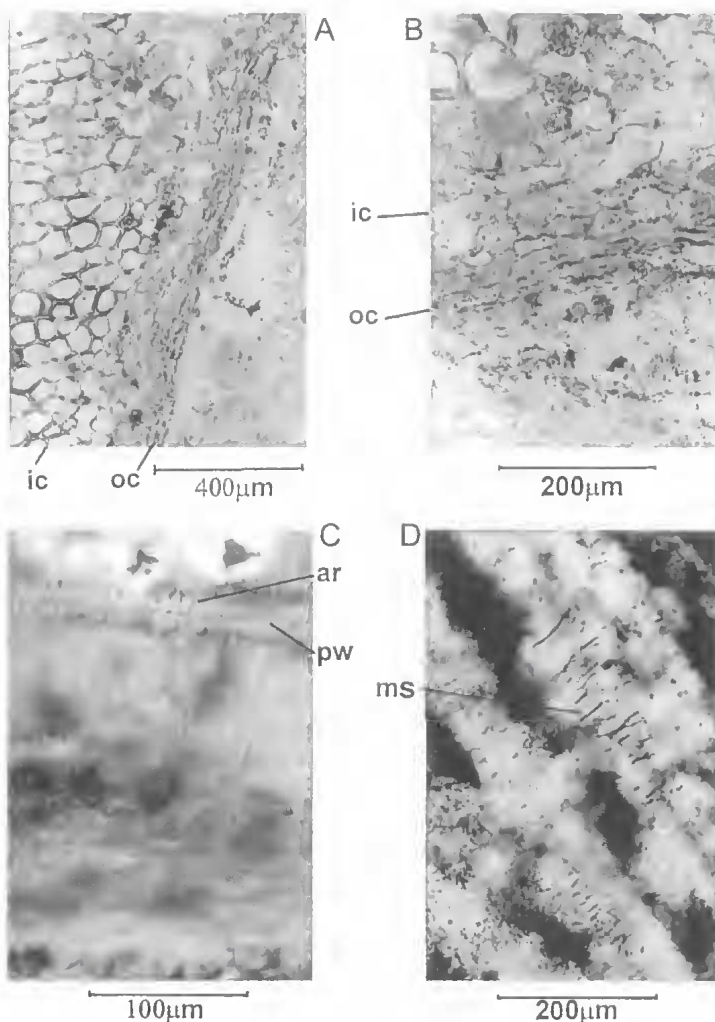


FIG. 4. Anatomical details of *Fanningopteris wyattii* gen. et sp. nov. A, B, transverse sections of cortex. C, longitudinal section of portion of tracheid element with annuli preserved. D, longitudinal section of portion of tracheid element with magnetite strand deposited on primary wall. a, annular ring; ic, inner cortex; oc, outer cortex; ms, magnetite strand; pw, primary wall.

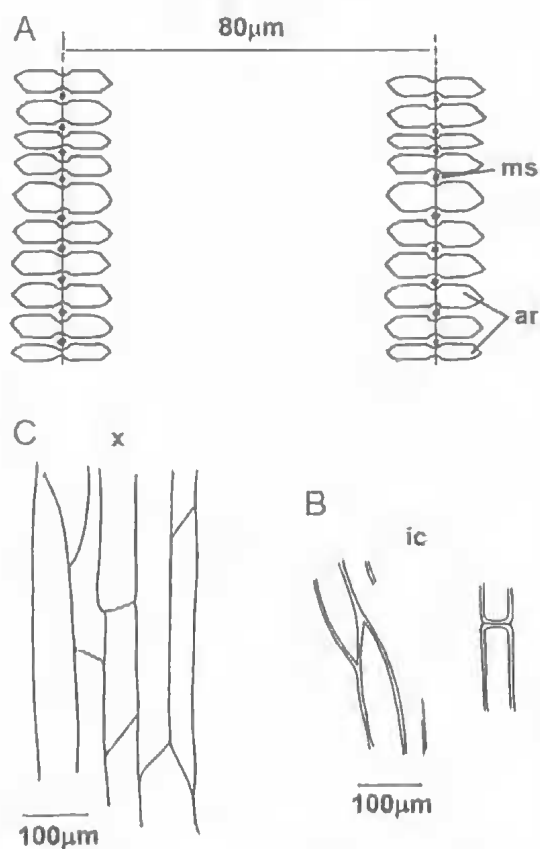


FIG. 5. Tracheid elements and cortical cells of *Fanningopteris wyattii* gen. et spec. nov. in longitudinal section. A, diagrammatic representation of site of deposition of magnetite on primary wall of tracheids element. B, disposition of end walls of inner cortical cells. C, disposition of end walls of tracheid elements. a, annuli; ms, magnetite strand.

stems have been cut transversely. The presence in the section of an axis with two steles suggests it has been cut between the position of the stele dichotomising and the separation of the daughter axes. Whenever two steles (Fig. 2) are present in an axis they differ in size and so are likely to be associated with daughter axes of different diameters a situation that may be observed with the frond segments of extant species of *Lygodium* another protostelic genus.

The habit of *Fanningopteris* is uncertain due to the limited material available. From the appearance of the vascular strands in transverse and vertical section it is apparent the axes, although flexuous and intertwining, are more or less erect and closely packed. They are thereby mutually supportive, but in addition gain

mechanical support from the thick-walled cells of the outer cortex and the ribbing of the axes. Further support may have been afforded by the interlacing of the adventitious roots and rhizomes. This information is, however, inadequate for reconstructing the habit of *F. wyattii*, because it is impossible to know which part of the plant, in terms of height, it represents. If it is the basal parts of the plant that have been preserved, and the rhizomes indicate this may be so, *F. wyattii* would have resembled the Lower Devonian *Zosterophyllum myretonianum* (Gensel & Andrews, 1984) or some modern *Schizaea* species.

Otherwise, *Fanningopteris* would have resembled the Lower Carboniferous *Austroclepsis australis* or one of the Cretaceous species of *Tempskya*. These plants were characterised by false stems which formed as a result of the linking together of the basal portions of several intertwining axes in a felt of adventitious leaving the distal portions free as with the modern tree-fern *Todea barbara*.

To distinguish between relative probabilities of these two reconstructions, recourse was had to a comparison of the maximum stem diameter of *F. wyattii* with those of several species some of which had and others did not have false-stems. The maximum diameters of the axes of the several taxa considered are listed in Table 1.

From the Table it is clear that whereas the maximum diameters of species with free standing axes vary from 1.1-4.0mm those species whose axes become associated into false-stems vary in maximum diameter from 3.5-18.0mm. Therefore, *F. wyattii* with a maximum axis diameter of 4.7mm, qualifies, albeit with some uncertainty, for membership of the false-stem group. Further support for believing the species developed false-stems is afforded by its appearance in transverse section, for other than in the sizes of their axes *F. wyattii* and *Austroclepsis australis* are morphologically similar, though differing in anatomy.

DISCUSSION

In the absence of reproductive structures the affinities of *F. wyattii* must be determined solely on the basis of vegetative anatomy. Here all the erect axes have been accepted as stems because they are anatomically similar rather than being of two kinds as would be expected if some were cauline and others petiolar in origin. Having dichotomously branched, leafless stems with

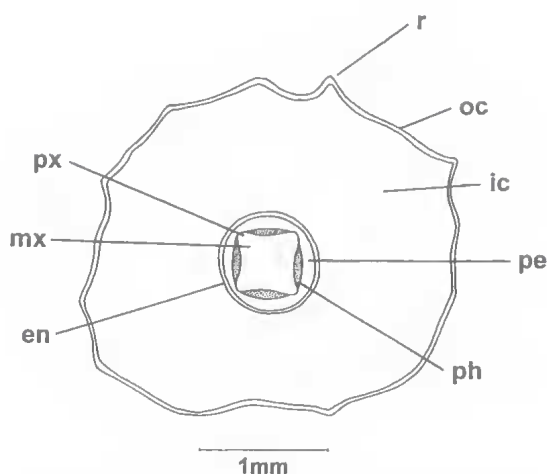


FIG. 6. Reconstruction of a representative axis of *Fanningopteris wyattii* gen. et sp. nov. in transverse section. en, endodermis; ic, inner cortex; mx, metaxylem; oc, outer cortex; pe, pericycle; ph, phloem; px, protoxylem, r, rib.

exarch protoxylem the species has much in common with members of the Zosterophyllophyta but is excluded from that group because of its adventitious roots.

The relations of *F. wyattii* have therefore been sought amongst the ferns as defined by Taylor & Taylor (1993) who list five Orders as having been recorded from Devonian sediments.

The vasculature of all taxa assigned to these Orders is a protostele. Species of Cladoxylales and Iridopteridales have primary xylem strands that are deeply lobed in transverse section whereas those of the Rhacophytales are bar-shaped with peripheral loops at the ends and those of the Zygopteridales are elliptical. Therefore *F. wyattii* is not a candidate for membership of any one of these four Orders. However, notwithstanding its apparent lack of apophlebiae, because its axes are not separable anatomically into stems and petioles and the xylem strands are quadrangular or triangular in transverse section, the species may be accommodated in Stauropteridales.

Within the Order *F. wyattii* has more in common with *Rowleya trifurcata* than any species of the other two genera. Attention has been drawn above to the similarity of the tracheid elements of *Fanningopteris* to those of *Gosslingia* (Zosterophyllophyta) and in his description of *Rowleya* (Long, 1976) noted that although there is a case for placing the genus in

TABLE 1. The maximum stem diameters of *Fanningopteris wyattii* gen. et sp. nov. and those of some fossil and living taxa with free-standing axes and false-stems. (1) Sahni (1929), (2) Ash & Read (1976), (3) Erwin & Rothwell (1989), (4) Long (1976), (5) Kenrick & Edwards (1988), Taylor & Taylor (1993).

Taxon	Maximum axis diameter (mm)
<i>Fanningopteris queenslandica</i>	4.7
Axes Freestanding	
<i>Gosslingia breconensis</i> (5)	3.0
<i>Sawdonia ovata</i> (6)	4.0
<i>Psilotum nudum</i>	3.7
<i>Stauropteris biseriata</i> (3)	3.2
<i>S. oldhamia</i> (3)	3.4
<i>S. burntislandica</i> (3)	2.0
<i>S. herwickensis</i> (3)	2.5
<i>Gillespica randolphensis</i> (3)	1.1
Axes aggregated into false-stems	
<i>Austroclepsis australis</i> (1)	18.0
<i>Tempskya wessellii</i> (2)	5.0
<i>T. rossica</i> (2)	7.0
<i>T. superba</i> (2)	15.0
<i>T. grandis</i> (2)	6.0
<i>T. wyomingensis</i> (2)	8.0
<i>T. zolleri</i> (2)	8.0
<i>T. minor</i> (2)	3.5
<i>T. knowltoni</i> (2)	3.5

the Stauropteridales, because of its branching habit and lack of roots it could belong to a more primitive group allied to Psilotaceae.

It is accepted that *F. wyattii* is best included in the Stauropteridales until the structure and arrangement of its sporangia are known. On the basis of this assumption the Cultivation Gully specimen is only the second record of the Order from the Devonian, all others being from the Carboniferous.

The other Devonian record is that of *Gillespica randolphensis* from the Hampshire Formation near Elkins in West Virginia. This Formation is Famennian (Oliver et al., 1967) and so is about 15 My younger than the Givetian sediments at Cultivation Gully.

Whether *F. wyattii* would be included in the Stauropteridales were its spores and sporangia known is a matter of conjecture.

Likewise, whether the Order represents a single phylogenetic lineage or an artificial assemblage of simple plants with similar

morphologies and anatomical features' (Erwin & Rothwell, 1989) is uncertain. Nonetheless in reporting on a cladistic analysis of vascular plants Rothwell (1996) noted that, with the exception of *Aglaophyton*, the Stauropteridales are the sister group to all other vascular plants. Therefore, the discovery of well-preserved vegetative specimens of *F. wyattii* at a readily accessible locality is important for further searching may reveal the presence of fertile material. Such an exciting discovery would contribute data critical for determining the phylogenetic affinities of all Devonian ferns.

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